A PHYLOGENETIC COMPARISON OF THE MAXILLÆ THROUGHOUT THE ORDERS OF INSECTS.

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Since no comparative study of any structure, or set of structures, has been made in all of the insectan orders (considerations of the apterygotan orders, and of the apterous pterygotan orders, were naturally not included in the admirable studies of Comstock, Handlirsch, Tillyard, and others, who have sought to apply a uniform terminology to the wing veins of insects), I would present in the following discussion, the principal modifications of the maxillæ met with in the various insectan orders, including the Apterygota, as well as the wingless and winged Pterygota. Furthermore, since such a comparative study should always be made from the standpoint of phylogeny, I would also point out wherein the evidence of relationships gained from a study of the maxillæ is in complete accord with the conclusions regarding the interrelationships of insects reached through a study of the wings (Can. Ent., 1922, LIV, p. 206), and other features of the body, used as a basis of comparison, thus furnishing further support of the correctness of these conclusions by means of confirmatory evidence from other sources.

The leg-like mouthpart-limbs of the Trilobita (which are just like the trunk limbs, in these forms) are of far too primitive a type to be the immediate precursors of the modified mouthpart-limbs which form the mandibles, maxillæ, and other trophi in insects; and, as I have pointed out in several papers (Jour. N. Y. Ent. Soc., 1921, XXIX, p. 63; Psyche, 1921, XXVIII, p. 84; Proc. Ent. Soc. of Washington, 1922, XXIV, p. 65, p. 153, etc.), there must have been a long series of intermediate stages, before the insectan types were evolved—and the Crustacea are the only known forms, which furnish these necessary intermediate stages connecting the insectan types with the trilobitan, and other structurally primitive types.

The view which I have encountered everywhere, among American entomologists at least, is that the immediate precursors of the Insecta are the Chilopoda; but I must confess that despite my absolute willingness to do so, I have been utterly unable to derive any of the structures of insects from chilopodan prototypes—and this naturally applies to the maxillæ as well as to the other structures of the body. Even the most cursory glance at the chilopodan maxilla shown in Fig. 16, for example, should convince anyone of the utter impossibility of deriving a typical insectan maxilla (such as the one shown in Fig. 4 or Fig. 5) from such a source—yet the chilopod maxilla shown in Fig. 16 is quite typical of chilopods in general, in all essential features! If we are to derive the insectan type of maxilla from some prototype or other, it is surely quite reasonable to demand that the prototype in question shall at least bear some faint resemblance to its supposed derivative, but I do not know of any chilopod whose maxillæ (or any other structures, for that matter) would fulfil these conditions—and even the symphylan and other "myriopodan" maxillæ figured by Latzel, 1880, Hansen, 1903, and others, would not serve as suitable prototypes for the typical insectan maxillæ. Among the Crustacea, on the other hand, we find some types of maxillæ and maxillipeds which are structurally just like the maxillæ of insects, while others of the Crustacea approach the types occurring in the lower arthropodan forms, and the Crustacea thus furnish not only the necessary prototypes of the structures of insects, but they also furnish the necessary (and only available) intermediate stages connecting insects with the lower Arthropoda—and a study of these Crustacea enables us to correctly interpret the homologies of the various structures occurring in insects.

If, then, instead of wasting our time in the fruitless contemplation of a chilopod's maxilla (Fig. 16) we compare a typical insectan maxilla such as the one shown in Fig. 4 with the crustacean maxilliped shown in Fig. 3 (which is essentially similar to the maxilla of the same crustacean, shown in Fig. 2) it is at once quite obvious that the cardo *cp* of the insect shown in Fig. 4 corresponds to the coxopodite *cp* of the crustacean shown in Fig. 3, while the stipes *bp,* with its lacinia *be,* of the insect shown in Fig. 4 corresponds to the basipodite *bp* with its endite *be* of the crustacean shown in Fig. 3. Similarly, the palpifer *ip* with its galea *ie* of the insect shown in Fig. 4, corresponds to the ischiopodite *ip* with its endite *ie,* of the crustacean shown in Fig. 3; and the four segments *me, crp, pp,* and *dp* of the maxillary palpus of the insect shown in Fig. 4, correspond in every way to the four segments *me, crp, pp,* and *dp,* of the maxilliped palpus (or endopodite) of the crustacean shown in Fig. 3—and the remarkably close correspondence in these two classes of arthropods extends not only to the number of segments involved, but also to the relative proportions of the individual segments of the structures compared.

The terminal portion *dl* of the lacinia *la* of an insect such as the one shown in Fig. 26 (or in Figs. 21, 22, etc.) may be referred to as the distilacinia (the basal portion *bl* of the lacinia being the basilacinia) and this distilacinia in a number of primitive insects bears a fringe, or fimbrium, made up of several modified spine-like structures corresponding in a remarkable fashion to the modified seta or spine-like structures occurring at the tip of the second endite of various crustacean maxillæ (*e.g.,* at the tip of the endite *ie* of Fig. 2). The remarkable correspondence in the minute details of the structures of the two groups of arthropods is at once apparent when we compare the fringe of the distilacinia of the insect shown in Fig. 24, with the fringe of the second endite of the crustacean shown in Fig. 25, in both of which there occur tooth-like "laciniadentes" labeled *a,* a longer "midappendix" labeled *b,* and pectinate "lacinulæ" labeled *le.* The "midappendix" labeled *b* in the crustacean shown in Fig. 17 is longer and more like that of the insect shown in Fig. 24 than is the case with the crustacean shown in Fig. 23; but the other parts of the fringe of the endite of the crustacean shown in Fig. 25 are more like the insect shown in Fig. 24 than is the case with the crustacean shown in Fig. 17.

The fringe or terminal structures labeled *a, b* and *le,* in the distilacinia of the Machilid insect shown in Fig. 15 are just like those bearing the same labels in the Podurid insect shown in Fig. 24 and the same types of structures occur in the terminal fringes of the distilaciniæ of other apterygotan insects such as the Entomobryid shown in Fig. 14, the Sminthurid shown in Fig. 8, the Sminthurid shown in Fig. 6, the Podurid shown in Fig. 12, etc., and even the Lepismatid insect shown in Fig. 9, has the marginal structures *a, b* and *le.* quite similar to those of the Entomobryid shown in Fig. 14 and the other Apterygota mentioned above. These parts in the Lepismatids and Machilids are so similar to those of the other Apterygota (and they are so different from the lacinial fringes of the maxillæ of the Pterygota) that they lend additional weight to the many features which clearly indicate that the Lepismatids and Machilids (*i.e.*, the "Thysanura") are true Apterygota, and cannot be regarded as degenerate Pterygota, as Handlirsch and others are inclined to believe.

In addition to many other features of the body, the structure of the maxillæ of the Protura clearly indicates that the Protura are true apterygotan insects and that they are not very closely related to the "Myriopoda," as is claimed by certain investigators. If one compares the maxilla of the proturan shown in Fig. 22 with the maxilla of the "myriopod" shown in Fig. 16 it is at once apparent that there is no great similarity between the two, while on the other hand, if one compares the maxilla of the proturan shown in Fig. 22 with the maxillæ of the other apterygotan insects shown in Figs. 23, 21, 18, etc., the similarity is very striking. Thus the cardo *ca* of Fig. 22 is just like the cardo *ca* in Figs. 23, 21, 18, etc. The stipes *st,* with its lacinia *la,* of Fig. 22, is not essentially different from these structures in Figs. 18, 21, 23, etc., and the palpifer *pf,* with its galea *ga* of Fig. 22 is very similar to the palpifer *pf* with its galea *ga* in Figs. 23 and 21, while the maxillary palpus *mp* of Fig. 22 is quite like its homologue *mp* in Fig. 23. The evidence of the maxillary structures would therefore be in complete harmony with that furnished by other structures indicating that the Protura are true apterygotan insects.

As was mentioned above, the maxillæ of the Protura, Poduridæ, Sminthuridæ and Entomobryidæ are quite similar, and the evidence of the maxillary structures would be in harmony with the grouping of these insects into a proturoid division (Panprotura) of the subclass Apterygota based upon the nature of the body in general in these insects.

The Japygidæ and Campodeidæ (sensu lato) are somewhat intermediate between the proturoid Apterygota mentioned above and the thysanuroid Apterygota; and the maxilla of *Japyx* (Fig. 23), for example, is more like the maxillæ of the proturoid insects (Figs. 22, 21, 18, etc.) than it is like the maxillæ of the thysanuroid insects (Figs. 26 and 10), in many respects—as is also true of the head and mouthparts in general of the Japygidæ and Campodeidæ. On the other hand, the presence in the Japygidæ and Campodeidæ of cerci, styli, and other abdominal structures which are not developed in the proturoid insects makes me more inclined to group the Japygidæ and Campodeidæ with the thysanuroids than with the proturoids, although I would not insist upon this grouping and it would doubtless be more exact to place the Japygids and Campodeidæ in a group intermediate between the proturoids and thysanuroids. For the sake of convenience, however, I have grouped them in the thysanuroid division (Panthysanura), in the following discussion. The lacinial fringe, *le,* of *Japyx* (Fig. 23) is more like that of certain Lepismatid thysanuroids such as the Lepismatids related to *Nicoletia,* than it is to the lacinial fringe of the proturoids, and the galea and palpifer *ga* and *pf* of *Japyx* (Fig. 23) is more suggestive of the Lepismatids than it is of the proturoids, so that the maxillæ of the Japygidæ and Campodeidæ may be said to be intermediate between the proturoid and thysanuroid types in some respects. The maxillary palpus was omitted in the drawing from which Fig. 13 was made but a comparison of the maxilla of *Campodea* shown in Fig. 13 with the maxilla of *Japyx* shown in Fig. 23 very clearly indicates that *Campodea* and *Japyx* are members of the same order of insects as is also borne out by a study of the structural details of the body in general so that the orders Rhabdura and Dicellura (in which the Campodeidæ and Japygidæ are frequently placed) should be merged into one.

Machilis (Fig. 26) is an extremely primitive thysanuroid insect, and in its maxilla the palpifer *pf* retains its primitive condition as a distinct segment not yet united with the stipes *st,* which is very like the stipes of the proturoids (Fig. 18, 21, 22, etc.) in its general character. The lacinial fringe labeled *a, b,* and *le,* in the Machilid shown in Fig. 15 is also strikingly similar to these structures in the proturoid insect shown in Fig. 24 and the huge development of the maxillary palpus *mp* (which, however, is composed of seven segments—a most unusual number) probably denotes the retention of a very primitive condition. These features are in harmony with many other facts which indicate that the Machilidæ are much more primitive insects than is usually supposed to be the case, and they have preserved a number of characters present in the ancestral insects, very suggestive of their crustaceoid prototypes. The Machilidæ also approach the Lepismatidæ quite closely (Fig. 10), and the

Lepismatidæ are very like the forms giving rise to the pterygotan insects, in many respects.

The maxillæ of the Lepismatidæ (Fig. 10) are astonishingly like the maxillæ of certain lower Pterygota, and in fact are more pterygotan than apterygotan in character (although this is not true of the maxilla of *Machilis* shown in Fig. 26, which is also a thysanuroid apterygotan). Thus the cardo, *ca,* of Fig. 10 tends to become divided into two sclerites *bc* and *dc;* the palpifer *pf* tends to unite with the stipes *st,* which thus appears to bear both galea *ga* and lacinia *la;* the lacinia *la* is quite pterygotan in character, and the number and relative proportions of the segments of the maxillary palpus *mp* of the insect shown in Fig. 10, are strikingly pterygotan. The fringe of the lacinia of the Lepismatid insect shown in Fig. 7 is also very like that of the pterygotan insect shown in Fig. 47, especially in the nature of the appendage *b.* On the other hand, the structures *a, b* and *le* of the lacinial fringe of the Lepismatid insect shown in Fig. 9 are more apterygotan (compare with Fig. 14), and taking the structure of the body as a whole, the Lepismatids are much nearer to the Machilids than they are to the Pterygota—and the Machilids are "out and out" Apterygota. When we take all of their structures into consideration, the Lepismatids are also more apterygotan than pterygotan, but in their maxillæ and certain other features, they furnish excellent annectant forms connecting the Apterygota with the Pterygota.

In comparing the maxillæ of the Pterygota, I shall have occasion to refer to areas and subdivisions which are possibly not familiar to anyone who has not made a special study of the maxillæ of insects, and on this account it may be well to briefly describe the principal parts of a typical pterygotan maxilla. For this purpose the maxilla of the orthopteran *Gryllus* (Fig. 33) will serve as well as any to illustrate the main features of value in comparing the various pterygotan types.

The cardo of *Gryllus* (Fig. 33) is composed of a basal area or basicardo *bc,* and a distal area or disticardo *dc,* and in addition to these, there may occur a cardomarginal area *cm,* which, however, is of no great importance, from the standpoint of comparative anatomy, while the basicardo and disticardo occur in long series of insects extending even to the higher Pterygota. The first designations to be applied to the areas *bc* and *dc* were the terms "paracardo" and "eucardo" (Psyche, XXIII, 1916, p. 83); but it is preferable to apply the designations basicardo and disticardo to these areas in all insects. As shown by DuPorte, 1920, and others, the basicardo is connected with the tentorium by a tentorio-basicardine muscle, and the disticardo is connected with the tentorium by a tentorio-disticardine muscle, both of which serve as adductors ("closers") of the maxilla. The cardo usually articulates with the hypostomal region of the head capsule by means of a cardocondyle *cc;* and a condylar groove in this area of the cardo usually receives a ridge or projection of the margin of the hypostomal region of the head capsule. The cardoprocess *cpr* is a process of the basal portion of the cardo to which muscles are attached by means of the cardotendons *ct*—such, for example, as the gena-cardotendon and postgena-cardotendon muscles, which serve as abductors ("openers") of the maxillæ by pulling down upon the cardoprocess, while the cardocondyle *cc* serves as fulcrum. Internally, the division of the cardo into a basicardo and disticardo is frequently marked by a transcardo plica or transverse infolding of the integument of the cardo, forming an internal ridge-like structure to which the adductor muscles may be attached. This division of the cardo into a basicardo and disticardo (*bc* and *dc* of Fig. 33) may possibly correspond to the division of the basal segment *cp* of the crustacean maxilla shown in Fig. 2; but this point has not as yet been definitely determined. A cardomarginal plica demarks the cardomarginal region internally.

The stipes forms the main portion of the "body" of the maxilla, and the palpifer *pf* tends to unite with it more or less closely in the Pterygota. The stipes is divided into a true stipes, or eustipes, *eus,* and a parastipes, *pas* (first defined in Psyche, 1916, p. 83), and this division persists in many types of insects. An internal parastipital plica or infolding of the integument along the line demarking the parastipes *pas* forms an internal ridge to which the tentorio-parastipital muscles (extending from the parastipital region to the tentorium, and serving as flexors ("closers") of the maxillæ, may be attached. The parastipes *pas* of Fig. 33 may possibly correspond to the narrow chitinized region *pas* of Fig. 2; but this again is pure speculation. The eustipes *eus* of Fig. 33 may be divided into a basal region *bs* or basistipes, a distal region *ds* or dististipes, and a median region or mediostipes, labeled *ms* in Fig. 35, by the formation of sutures in the region *eus* of Fig. 33 (in which the beginnings of the formation of these sutures can be detected, while they have become completely formed in Fig. 35). Fig. 36 presents an intermediate condition in which the parastipital region *pas* (which is distinct in Fig. 33) tends to unite with the median region *ms* to form the larger median region *ms* of Fig. 35. A stipito-lacinial muscle from the stipes to the tendon at the base of the lacinia serves to flex the lacinia, while a stipito-galeal muscle from the stipes to the galea serves to flex the galea, and stipito-palpal muscles from the stipes to the basal segment of the maxillary palpus aid in extending and flexing the palpus. It is possible that the tension of the above mentioned muscles may play some rôle in the division of the eustipes into areas, but this is not very probable.

The lacinia may bear apical laciniadentes *ld* or tooth-like processes for holding and comminuting the food, and the appendage labeled *b* in Fig. 33 may be a modified tooth-like appendage, or a modified "lacinula" such as occur on the laciniæ of such insects as the one shown in Fig. 24 (*i.e.,* the structures labeled *le* in Fig. 24—of which the structure labeled *b* in Fig. 24 may be a modification). At any rate, the structure labeled *b* in Fig. 33 appears to be homologous with the structure bearing the same label in Fig. 47. The laciniafimbrium or fringe of hair-like, bristle-like, or spine-like structures bordering the lacinia has not been figured in most cases, since it is not very important for the purpose of demonstrating the affinities of the insects compared.

The galea is divided into a basal segment or basigalea *bg* and a distal segment or distigalea *dg* (first so designated in Psyche, 1916, p. 83) in Fig. 33, and this division of the galea into two segments occurs in a wide series of insects. The distal segment of the galea frequently bears a galeal sensarea, or sense area which usually remains membraneous and is provided with sensory organs in many insects. The distal segment of the galea bears a galeafimbrium or fringe in many coleopterous, neuropterous, and mecopterous insects, and the fringe of the galea and that of the lacinia are frequently modified for feeding purposes.

The maxillary palpus is usually five-segmented, with the basal two (basimeres) small and subequal; the third (intermere) is frequently long, and the distal two (distimeres) are usually somewhat shorter, and subequal in size. The terminal segment of the maxillary palpus frequently bears at its tip a palpal sensarea which is usually membranous and richly provided with sense organs. Endomeral flexor and extensor muscles (within the palpal segments) serve to flex and extend the maxillary palpus.

Some of the modifications of the maxillæ in the various pterygotan orders are as follows. The cardo of a typical Odonatan (Fig. 30) is divided into basicardo and disticardo (*bc* and *dc*); but the parastipital region is not clearly demarked from the remainder of the stipes in most cases. The lacinia frequently bears numerous tooth-like processes, and the galea shows traces of two segments in many cases. The maxillary palpus is wanting in all of the Odonata I have examined (unless the structure here interpreted as the galea is in reality the maxillary palpus—in which case there is no galea), and this is possibly characteristic of the order.

In the Ephemerida (Fig. 31) the cardo may show traces of a division into basicardo and disticardo, and the stipes may show indications of a division into eustipes and parastipes, although I am not certain that the area labeled *pas* in Fig. 31 is strictly homologous with the areas bearing this label in other figures. In all of the Ephemerida which I have been able to examine, the galea and lacinia appear to unite to form a single maxillary "mala"; but in the naiads of the primitive New Zealand ephemerid *Oniscigaster* (Fig. 31) collected by Dr. J. W. Campbell and turned over to me to study by Dr. C. P. Alexander, the mala of the maxilla is divided by a well-defined suture which I have interpreted as the line of demarcation between the uniting galea *ga* and lacinia *la*. The union of the galea and lacinia is possibly characteristic of the order Ephemerida.

Certain ephemerid naiads (*i.e.*, immature forms) exhibit tooth-like processes of the lacinia very suggestive of those occurring on the lacinia of certain Odonata (Fig. 30); but the maxillæ of the Ephemerida are not as similar to those of the Odonata as might be expected from the fact that the Ephemerida and Odonata may be grouped in a superorder (Panarchiptera) on other grounds. The maxillæ of the Odonata are decidedly aberrant, and the same is true, to some extent, of the maxillæ of the Ephemerida, so that the general aberrant nature of the insects in question may account for the lack of similarity between the two groups in certain features.

As may be seen in Fig. 1 the insects next above the thysanuroids are the palæodictyopteroid insects comprising the archaic Pterygota (division "Archipteradelphia") which include the Palæodictyoptera with their immediate relatives, together with the Prodonata, Odonata, Protephemerida and Ephemerida. In most of these insects the fore and hind wings are alike (homonomous), and they are unable to lay the wings flat along the top of the abdomen when at rest. Since they are among the most primitive of the Pterygota in many respects, I was much disappointed to find that the maxillæ of the Ephemerida and Odonata are rather highly modified, so that the evidence of the maxillæ alone would not indicate the true primitive nature of the insects in question, and we are dependent upon other features to determine their position in the scale of development indicated in Fig. 1.

The orthopteroid insects which are accorded the position immediately above the palæodictyopteroids in Fig. 1 constitute the division Orthopteradelphia, or lower pterygotan insects (the palæodictyopteroids constitute the archaic pterygotan insects). These orthopteroid insects or lower Pterygota tend to exhibit a heteronomous condition of the wings (*i.e.,* fore wings differing from the hind ones) due to the tendency toward the development of an anal fan in the hind wings. The wings are capable of being laid flat along the back of the abdomen.

The orthopteroid insects may be divided into three superorders called the Panplecoptera (comprising the Plecoptera, Embiids, and their immediate relatives), the Panorthoptera (comprising the Orthoptera, in the restricted sense, the Protorthoptera, the Phasmids, and the Dermaptera, with their immediate relatives) and the Panisoptera (comprising the Protoblattids, Blattids, Mantids, and the Isoptera, with their immediate relatives). Of these, the Panorthoptera and Panisoptera may be regarded as a single superorder; but for the sake of convenience, I shall treat them as separate groups in the following discussion. All of these insects are derived from the common Protoblattid-Protorthopteran stem, and hence exhibit marked intergradations making it very difficult to determine where to draw the dividing line separating them into definite groups.

The maxillæ of the Panplecoptera (Plecoptera, Embiids, etc.) are not as similar as one would expect from the marked similarity in wing-venation, terminal structures of the male insects, character of the thoracic sclerites and other features in the Embiids and Plecoptera, for example; but the character of the galea *ga* in the primitive Plecopteran shown in Fig. 44 (which was given to me by Dr. Tillyard) is very similar to the one of the Embiid shown in Fig. 40 (drawn from specimens collected by Dr. Wheeler and Dr. Bailey), and the nature of the lacinia *la* is practically the same in both Figs. 44 and 40. The cardo *bc* and *dc* is rather slender and elongate in both; but other than in the features mentioned above the Embiids and Plecoptera are disappointingly unlike in the general character of their maxillæ.

In the slenderness of their laciniæ *la* and galeæ *ga*, the Plecoptera shown in Figs. 44 and 46 are rather suggestive of the Dermaptera (Fig. 35), and the Plecopteran shown in Fig. 46 has a small terminal micromere *mm* similar to the micromere *mm* at the tip of the palpus of the Dermapteran shown in Fig. 35. The slender basigalea *bg* and distigalea *dg* of the Plecopteran shown in Fig. 46 are suggestive of the slender basigalea *bg* and distigalea *dg* of the Coleopteran shown in Fig. 37, and the formation of a chitinized plate or basimaxilla *bm* in the basimaxillary membrane at the base of the maxilla of the Plecopteran shown in Fig. 44 is also suggestive of the basimaxilla *bm* of the Coleopteran shown in Fig. 5. A similar basimaxillary plate *bm* occurs in the Isopteran shown in Fig. 45. The maxillæ of the Plecoptera therefore exhibit similarities to those of the Embiids, Dermaptera, Coleoptera, and Isoptera, and they are also suggestive of the maxillæ of the true Orthoptera such as those shown in Figs. 41, 34, etc. These facts are quite in harmony with the evidence from other sources which indicates that all of the forms in question are descended from the common Protorthopteran-Protoblattid stock. From this same stock the Phasmids were derived, and this probably accounts for the resemblance between the maxillæ of the Embiids (Fig. 40) and the Phasmids although the primitive Phasmid shown in Fig. 39 (drawn from a specimen given me by Dr. Ferris) does not illustrate this marked resemblance between the Phasmids and Embiids as well as might be desired.

The maxillæ of the Panorthoptera (*i.e.*, true Orthoptera, Phasmids, Dermaptera, etc.), present some features of considerable interest from the standpoint of the origin of the higher Pterygota such as the Coleoptera, etc., and the hints which they offer are of considerable value. As was mentioned in the preceding discussion, the Gryllid shown in Fig. 33 illustrates the beginning of the breaking up of the eustipes *eus* into a basistipes *bs,* a dististipes *ds,* and a mediostipes *ms* which is still distinct from the parastipes *pas* in Fig. 34, but unites with it to form the enlarged mediostipes *ms* of Fig. 35. In the Dermapteran shown in Fig. 35, and the Orthopteran shown in Fig. 34 we clearly have the prototypes of the coleopterous maxillæ such as those shown in Figs. 37 and 36, in so far as the formation of the peculiar sclerites *pf, bs, ms* and *ds* is concerned (a condition occurring in no other insects so far as I am aware), and the marked similarity in these peculiar features clearly indicates that the Coleoptera, Dermaptera and Orthoptera sprang from common ancestors which were very like the ancestral Protorthopteran-Protoblattid stock which gave rise to the Orthoptera and Dermaptera (as well as to the Plecoptera and Embiida) at a lower level than that at which the Coleoptera branched off. The striking similarity in the character of the cardo, stipital region, slender galea and lacinia, etc., of the insects shown in Figs. 34 and 35 is clearly in harmony with the evidence from other sources (such as the nature of the thoracic sclerites and appendages, cerci, etc.) pointing to the Orthoptera as the nearest relatives of the Dermaptera; and the two groups apparently sprang from a common source in the common Protorthopteran-Protoblattid stock. The character of the cardo and the long narrow palpifer *pf,* together with the presence of a micromere *mm* at the tip of the maxillary palpus are features which add to the evidence from other sources pointing to the fact that the Hemimeridæ (Fig. 28) are merely modified Dermaptera (Fig. 35).

The maxilla of the very primitive Orthopteran *Grylloblatta* shown in Fig. 41 (which was drawn from a specimen loaned by Dr. Walker) gives some evidence that at a very early stage of Orthopteran development there occured a slender lacinia *la* which was not overtopped by the slender galea *ga* (in which respect the maxillæ of the primitive Orthoptera were doubtless more like that of the Plecopteran shown in Fig. 44, than they were like the maxillæ of the Blattid shown in Fig. 47); and this primitive condition is also retained by the Dermapteron shown in Fig. 35 and the Orthopteron shown in Fig. 34. On the other hand, the galea *ga* of the Phasmid shown in Fig. 57 (which is a close relative of the primitive true Orthoptera) is broad and overtops the broad lacinia *la* as in the Blattids (Fig. 47) and their allies. The character of the cardo, stipital region, lacinia and galea of the maxilla of *Grylloblatta* would lend weight to the view that it is closely related to the true Orthoptera (Figs. 34, 33, 42, etc.) rather than to the claim made by other investigators who would place *Grylloblatta* nearer the Blattids and Mantids (Figs. 47 and 48). The maxilla of the Tridactylid (shown in Fig. 42) with its peculiar sclerite *lf* immediately proximal to the lacinia *la* is strikingly similar to the maxilla of the Tettigid shown in Fig. 43, thus lending further support to the view that the Tridactylidæ are much more closely allied to the Tettigidæ than they are to the Gryllidæ (as some investigators claim). The maxillæ of the Gryllidæ (Fig. 33) are very like the maxillæ of the Tettigoniidæ (the old "Locustidæ") such as the one shown in Fig. 32, and the maxillæ of the Tettigoniidæ are somewhat more like those of the "Acrididæ" (or Locustidæ, as they are now called) than the Gryllid maxillæ are. The maxillæ of some primitive Phasmids (Fig. 39) are more like those of the true Orthoptera, while the maxillæ of other Phasmids (Fig. 57) are somewhat more like those of the Blattids and Mantids (Figs. 47 and 48), thus lending weight to the view that the Phasmids are in a measure annectant between the Blattid-like forms and the true Orthoptera (and the lower phasmids, such as the one shown in Fig. 39, also approach the Embiid type shown in Fig. 40, thus indicating the synthetic nature of the Phasmids).

In the maxillæ of the Panisoptera (Blattids, Mantids, Isoptera, etc.) the galea *ga* is usually large and "fleshy" and overtops the lacinia *la*. The maxillæ of the Blattids (Fig. 47) are so like those of the Mantids (Fig. 48) that this would indicate that these insects should be grouped in a single order. The persistence in the Blattid shown in Fig. 47 of the pectinate "midappendix" labeled *b*, which occurs in certain apterygotan insects such as the one shown in Fig. 7, is a very primitive character; but the homologue of the structure labeled *b* in Fig. 47 probably also occurs in certain other members of the lower Pterygota (*e.g.*, Fig. 46, Fig. 33, etc.). The Isopteron shown in Fig. 45 is not as much like the Blattids and Mantids shown in Figs. 47 and 48 as one would expect. The presence in the Isopteron shown in Fig. 45 (drawn from a specimen given me by Dr. Bequaert), of the basimaxilla *bm* is a feature suggestive of the Plecopteron shown in Fig. 44, and a similar basimaxillary plate *bm* occurs in the coleopterous larva shown in Fig. 5. The maxillæ of the Isoptera would bear out the conclusion that the Isoptera are the representatives of the superorder Panisoptera which are approached the most closely by the members of the other superorders (such as *Grylloblatta* (Fig. 41), etc., among the Panorthoptera, *Oligotoma* (Fig. 40) among the Panplecoptera, etc.) and this is probably due to the fact that the Isoptera are as near as any Panisoptera are to the Protorthoptera, whose line of development is paralleled by that of the other superorders in question. The evidence of the maxillæ of the insects in question would be in harmony with that from other sources, which indicates that the Blattids, Mantids and Isoptera are the descendants of the common Protorthopteran-Protoblattid stock from which the other lower Pterygota were also derived (*i.e.,* they branched off at the point where the common Protorthopteran-Protoblattid stock began to diverge from the Palæodictyoptera).

The so-called higher Pterygota (Neuropteradelphia) are characterized by the fact that the wings are heteronomous, the fore wings being usually larger than the hind ones, and the wings are either laid flat along the abdomen when at rest or are held "rooflike" over it, in most cases. There are two principal superorders of higher Pterygota. These are the Panhemiptera (Hemiptera with the Homoptera, Psocids, Mallophaga, Pediculids, etc.) and the Panneuroptera which include the Neuroptera, Coleoptera and Hymenoptera, etc., together with a group of higher Neuropteroids composed of the Mecoptera, Diptera, Siphonaptera, Lepidoptera, Trichoptera, etc. These higher Neuropteroids have been grouped in a separate superorder, the Panmecoptera; but it might possibly be preferable to include them in the superorder Panneuroptera rather than place them in a distinct superorder.

Among the Panhemiptera (Psocids, Mallophaga, Anopleura, Hemiptera, etc.) the Psocids have retained the maxillæ in the most primitive condition occurring in the superorder, thus bearing out the evidence from other sources that the Psocids have departed as little as any from the condition approximating the original one for the superorder. In a previous paper (Can. Ent., 1922, LIV, p. 206) the Zoraptera were placed in the order Psocida (Parahomoptera) on account of the great similarity of the wings, head capsule, legs, testes, and other structures of the Zoraptera to those of the Psocids. I must admit, however, that the maxilla of a Zorotypid (suborder Zoraptera) such as the one shown in Fig. 38 (which was made from a specimen given me by Mr. Caudell) is of a much more primitive type than the maxilla of any other Psocid I have been able to find (*e.g.*, the one shown in Fig. 73 is typical of the Psocids in general). In fact, the maxilla of the Zorotypid shown in Fig. 38 is as "orthopteroid" as any of the higher insects, and on this account, I have placed the Psocoid insects (*i.e.*, the Psocids, Mallophaga, etc.) immediately above the "orthopteroids" in Fig. 1. The maxilla of the Zorotypid shown in Fig. 38 is very similar to that of the Phasmid shown in Fig. 39 and resembles the maxilla of the Embiid shown in Fig. 40 extremely closely. This resemblance is in harmony with the evidence of the wing veins, for example, which indicate that the Zoraptera were derived from Protorthoptera-like forbears closely allied to those from which the Embiids were derived, and the Phasmids were probably descended directly from Protorthopterous forbears. The Zorotypids approach the Isoptera in many respects, and one would expect that the maxilla of the Zorotypid shown in Fig. 38 would be more like that of the Isopteron shown in Fig. 45 than is the case. There is some resemblance between the two maxillæ, however, and this is probably due to the mutual relationship of the Zoraptera and Isoptera to the Protorthoptera (or to the Protorthopteran-Protoblattid stem from which both were descended).

The maxillæ of the Psocids (Fig. 73) are strikingly similar to those of the Mallophaga (Fig. 74), thus strongly supporting the view that the Mallophaga were descended from Psocid-like ancestors. As has been suggested by others, the stylet-like structure labeled *la* in Fig. 73 may represent the lacinia and if the structure labeled *la* in Fig. 73 is the lacinia, the structure labeled *la* in Fig. 74 must be the lacinia also. It is likewise quite probable that the structure labeled *la* in Fig. 72 is homologus with the structure labeled *la* in Figs. 73 and 74, and the maxillæ of the Thysanoptera (Fig. 72) approach those of the Psocids (Fig. 73) quite closely in their general features, thus adding further weight to the view that the Psocids and the Thysanoptera were descended from common forbears closely allied to the Protorthoptera. The mouthparts of the Anoplura (Fig. 76) are too highly specialized to offer any very serviceable clews as to immediate relatives of the group. The maxillæ of the Anoplura, however, are as near to those of the Mallophaga as any, and the nature of the mouthparts would not preclude their derivation from ancestral types related to the Mallophaga and Psocids—an ancestry which is indicated by other features of the body in general.

Although the Hemiptera appear to have lost them completely, the maxillary palpi are retained in both Thysanoptera (Fig. 72) and Psocids (Figs. 73 and 38), and the galea *ga* and stipites *st* of these insects are much more primitive than the structures labeled *ga* and *st* in the Homopteron shown in Fig. 75 (drawn from a specimen given me by Mr. Gowdey); and the evidence of the maxillary structures would indicate that the Psocids have departed much less than the Homoptera have from the ancestral condition of the Psocoid insects in general, although the phenomena of heterarchaism or heterospecialization (*i.e.*, the unequal primitiveness or specialization of the different parts of an organism, which frequently preserves some structures in a relatively primitive condition while other structures in the same individual may be rather highly specialized) make it very difficult to determine which insects are the more primitive when such unequally specialized forms are compared. The structure labeled *la* in Fig. 75 appears to be homologous with the structure labeled *la* in Fig. 73, and possibly represents the lacinia in which the basal portion has become invaginated to form a chitinous cup below the surface of the integument of the head capsule. The curled drum-like basal portion of the structure labeled *la* in Fig. 75 apparently represents the basal portion of the newly forming lacinia which fits into the old lacinia *la* of the nymph, in the fashion described by Snodgrass, 1922, in the cicada. The evidence of the maxilla would be in harmony with that from other sources indicating that the Hemiptera (with the Homoptera) were derived from ancestors which were the same as, or were very like those of the Psocids; and the grouping of the Psocids, Mallophaga, Anoplura and Hemiptera (with the Homoptera) into the superorder Panhemiptera is apparently a natural one.

The Coleoptera, Strepsiptera, Hymenoptera and Neuroptera with their allies form the Neuropteroid superorder Panneuroptera; and it is largely a matter of personal preference whether we restrict the superorder Panneuroptera to these forms or also include in the superorder Panneuroptera the higher Neuropteroids such as the Trichoptera, Lepidoptera, Mecoptera, Diptera, Siphonaptera and their allies (which might be grouped in a superorder Panmecoptera distinct from the rest of the Neuropteroids or holometabolous insects).

In some respects the Coleoptera are among the most primitive of the Neuropteroid insects, and as was pointed out above, their maxillæ Figs. 36 and 37) are strikingly similar to those of the Dermaptera (Fig. 35) and Orthoptera (Fig. 34), and even such highly modified parasitic Coleoptera as the Platypsllids (Fig. 29) and Leptinids (Fig. 27) appear to be modified along paths of specialization presaged in the parasitic Dermaptera of the family Hemimeridæ (Fig. 28). In this connection it should be remarked that the maxillæ of the Platypsyllids and Leptinids (Figs. 29 and 27) are so similar that, in addition to other features (such as the character of the head and body in general), the evidence of the maxillæ, etc., leaves no room for any doubt that both groups are anything else than modified Coleoptera (the generally accepted view), as I found out when I was able to compare specimens of both families loaned me by Dr. Cooley and Dr. Boving. It is not beyond the range of possibility that these two Coleopterous families have not departed far from the types which give rise to the Mallophaga and other Psocid-like forms, since the order Coleoptera took its origin very near the point at which the line of development of the Psocid-like forms arose from ancestors resembling the Protorthoptera, although the ancestors of the Coleoptera were identical with or very similar to the forms which gave rise to the Neuroptera (and occupied a position at the point where the common stem of the Protorthoptera and Protoblattida began to diverge from that of the Palæodictyoptera). The line of development of the Coleoptera is a rather aberrant one; but their nearest relatives appear to be the Neuroptera and Hymenoptera, and the maxillæ of certain Coleopterous larvæ are strikingly like those of certain lower Neuropterous larvæ (as may be seen by comparing Fig. 5 with Fig. 4, although the larvæ there shown are not the best fitted for illustrating the striking resemblance between the Coleoptera and Neuroptera).

The galea *ga* of the Neuropteron shown in Fig. 50 is rather slender and is divided into a basigalea *bg* and a distigalea *dg* suggestive of the condition exhibited by such Coleoptera as the one shown in Fig. 37; and, although this is not true of all Neuroptera (*e.g.*, the one shown in Fig. 49) there is a tendency in the Neuropterous maxillæ for the cardo to become quite slender (Figs. 50 and 51) and for the maxilla as a whole to depart rather widely from the Orthopterous type. The elongation of the maxillæ in the Neuroptera is apparently accomplished by the lengthening of the stipes *st* of Fig. 51, and of the lacinia *la* and galea *ga* which become long slender organs in the Neuropteron shown in Fig. 51. The lacinia *la* of the Neuropteron shown in Fig. 51 is longer than the galea *ga*, which is a rather unusual condition among insects in general; but a comparison with the other Neuroptera shown in Figs. 50 and 49 very clearly indicates that the structure labeled *la* in Fig. 51 is the true lacinia, and the structure labeled *ga* is the entire galea, which is divided into a basal and distal region (*bg* and *dg*) as in the Neuropteron shown in Fig. 50. When the cardo is long and slender in the Neuroptera (as in Figs. 50 and 51), it is still so oriented that its basal end is directed inward or toward the median plane of the body (*i.e.*, the maxilla is endocardine); but in the Hymenoptera, when the cardo is long and slender (as in Figs. 54, 55, and 56), its basal end is usually directed outward, or toward the lateral region of the body (*i.e.*, the maxilla is exocardine). In this respect, the maxillæ of even such primitive Hymenoptera as the one shown in Fig. 54, are rather highly specialized. In the very primitive Hymenopteron shown in Fig. 58 (which was drawn from specimens given me by Mr. Rohwer and Mr. Middleton), however, the cardo is more "normal."

In the Hymenoptera shown in Figs. 58 and 59, the galea *ga* is partially split into an inner lobe *eng* or endogalea and an outer lobe *exg* or exogalea; and this division into two lobes *exg* and *eng* apparently occurs in the galea *ga* of the Phasmid shown in Fig. 57 also. The Hymenoptera (together with the Neuroptera and Coleoptera) were apparently derived from ancestors in or extremely closely allied to the common Protorthopteran-Protablattid stock which gave rise to the Phasmids (and Isoptera also), and it is quite possible that both Hymenoptera (Fig. 58) and Phasmids (Fig. 57) may have inherited from a common source, the tendency for the galea *ga* to split into the external and internal lobes *exg* and *eng;* but this is pure speculation. At any rate, the Hymenoptera and the Phasmids are the only insects in which this tendency is exhibited, so far as I am aware, and I am unable to determine whether this tendency in the two orders is due merely to convergence or not. In many of the higher Hymenoptera, the lacinia *la* is greatly reduced (Figs. 55, 56, etc.), and the galea *ga* becomes folded upon itself, in some instances giving the appearance of the folds becoming adherent to each other so closely as to produce a more or less complete fusion of originally separate lobes. Whether these adhering lobes have any particular relation to the small lobes *exg* and *eng* of Fig. 58, is not clear. The maxillary palpi of certain of these higher Hymenoptera, such as the one shown in Fig. 54 or Fig. 55, appear to be composed of more than the usual five segments, and taken all in all, the maxillæ of the Hymenoptera exhibit the most remarkable specializations I have found among insects (with few exceptions).

For the sake of convenience, I shall refer to the higher Neuropteroids (*i.e.,* the Trichoptera, Lepidoptera, Mecoptera, Diptera, Siphonaptera, and their immediate relatives) as the "Panmecoptera," grouping them in a superorder distinct from the lower Neuropteroids or Panneuroptera (*i.e.*, the Neuroptera, Coleoptera, Strepsiptera, and Hymenoptera, with their immediate relatives), since the higher Neuropteroids are more closely related to each other than they are to the lower Neuropteroids, although they naturally intergrade with the lower forms, and the superorder Panneuroptera might be made to contain them also in a natural assemblage of holometabolous insects. It is very difficult to determine which of the higher Neuropteroids is the most primitive, since the Trichoptera have retained a very primitive type of venation in some instances (particularly in the anal region of the hind wings), and the maxilla of such Lepidoptera as the one shown in Fig. 77 is as primitive as any I have been able to find among the higher Neuropteroids; but taking their anatomy as a whole, the Mecoptera are doubtless the most primitive representatives of the higher Neuropteroids (Panmecoptera).

The maxilla of the primitive Mecopteron shown in Fig. 53 is quite "orthopteroid" in many respects, and it bears some resemblance to the maxilla of the Embiid shown in Fig. 40. In those Mecoptera in which the cardo is slender and elongate, as in Fig. 70 (drawn from a specimen given me by Dr. Tillyard), the cardo is turned outward (*i.e.*, the exocardine position obtains); but in most Mecoptera, the cardo is not elongate, and is turned inward (*i.e.*, the maxillæ are endocardine) as in Figs. 52, 53 and 60. Lengthening of the maxilla is usually accomplished by the lengthening of the stipes *st* which may be accompanied by a lengthening of the galea *ga* and lacinia *la* as in Fig. 52, or the galea and lacinia may not take part in the process, as in Fig. 60.

The Mecoptera approach the Hymenoptera in so many features that one might be led to think that the structures labeled *ga* and *la* in Fig. 60, instead of representing the galea and lacinia (as the labels would indicate), should be interpreted as representing the divided lobes *eng* and *exg* of the galea *ga* of the Hymenoptera shown in Figs. 59 and 58. That this view is entirely untenable, I am convinced for the following reasons. The structures labeled *ga* and *la* in the Mecopteron shown in Fig. 60 are entirely homologous with the structures labeled *ga* and *la* in the Mecoptera shown in Figs. 53 and 52, and what applies to one applies to all. If one compares the structures labeled *ga* and *la* in the primitive Mecopterous maxilla shown in Fig. 53 with the structures labeled *ga* and *la* in the primitive Hymenopteron shown in Fig. 54, or with the Embiid shown in Fig. 40, it is at once evident that the structures bearing the labels *ga* and *la* in all three insects are entirely homologous, and represent the galea and lacinia in all of them, including the Mecopteron shown in Fig. 53. Similarly, if one compares the structures labeled *ga* and *la* in the Mecopteron shown in Fig. 52 with the parts bearing the same labels in the Neuropteron shown in Fig. 51, it is quite apparent that the structures are entirely homologous in both, hence the structures labeled *ga* and *la* in Fig. 52 must represent the galea and lacinia, since their exact homologues *ga* and *la* in Fig. 51 represent the galea and lacinia, as may be seen by running back in the series of Neuroptera shown in Figs. 51, 50 and 49.

The evidence of the maxillæ would indicate that certain Neuroptera (Fig. 51) approach certain Mecopterous types (Fig. 52) more closely than is true of any other insects, and the evidence of the venation of the wings would also strengthen this view. On the other hand, the nature of the male reproductive organs and certain other features would indicate that the Hymenoptera also approach the Mecoptera very closely in many respects, and the type of Hymenopterous maxilla shown in Fig. 69 is very like that of the Mecopteron shown in Fig.

70 thus lending further weight to the latter view. I even find some features in certain Coleoptera which strongly suggest a close relationship to the Mecoptera; and all of these resemblances are doubtless due to the fact that the Mecoptera are descended from the same ancestors which gave rise to the lower Neuropteroids such as the Coleoptera, Neuroptera and Hymenoptera. As far as the maxillæ are concerned, the Neuroptera (Fig. 51) and Hymenoptera (Fig. 69) approach the nearest to the Mecopterous types (Figs. 52 and 70); although the tendencies exhibited by certain Coleoptera even in the maxillæ (Fig. 68) are not very different from those exhibited by the Mecoptera and Hymenoptera shown in Figs. 70 and 69.

Practically all of the structures of the Mecoptera are strikingly similar to those of some Diptera, and the evidence of the maxillæ bears out the relationship indicated, in a remarkable manner. Thus in the Dipteron shown in Fig. 71 and the Mecopteron shown in Fig. 70, the cardines *ca* are of the exocardine type, the character of the stipes *st* and galea *ga* is strikingly similar in both, and even the relative proportions of the segments of the maxillary palpi *mp*, both of which bear a peculiar sense organ *so* on the third segment, are remarkably similar down to the minutest details. Even the tendency for the stipes of both maxillæ to unite with the mentum of the labium to form a synstipites, as in the Dipteron shown in Fig. 71, is paralleled in the Mecoptera; and the comparative morphology of the various structures in the two groups of insects must convince even the most skeptical that the Mecoptera are the nearest living representatives of the types ancestral to the Diptera. I do not feel sure that the Diptera were descended from the Mecoptera themselves, however, since I am more inclined to consider that the Diptera were descended from the Neuropteroid forbears of the common stock which gave rise to the Mecoptera and Trichoptera, and these ancestral types quickly merged with the ancestral Neuroptera and Hymenoptera, so that features present in the Neuroptera and Hymenoptera may also be carried over into the Dipterous line of development. The series represented by Figures 68, 69, 70 and 71 is a very suggestive one, and the relationships indicated by the maxillæ of the insects in question are confirmed by the evidence of many other structures, so that the similarity is hardly due to convergence, but is rather the result of common tendencies inherited from a common ancestry.

In the Dipteron shown in Fig. 80, I have not interpreted the structure labeled *il* as the representative of the lacinia, since the structure in question is imbedded in the basimaxillary membrane in a fashion unknown in any lacinia, and the structure labeled *il* in Fig. 80 is apparently homologous with the interlora *il* of Fig. 55, which is a chitinous bar extending between the maxilla and the region of the hypopharynx. In Fig. 55, however, the maxilla was turned so far over that the structure labeled *il* appears on the other side, although if seen from another angle, it would appear to be on the same side of the maxilla as the structure labeled *il* in Fig. 80; and in the Hymenopteron shown in Fig. 69 the structure *il* is shown much better for comparison with Fig. 80, than is the case with the Hymenopteron shown in Fig. 55. In the Dipteron shown in Fig. 66, the galea *ga* has become enormously elongated, and this tendency for the galea to become very long also occurs in many other Holometabola, such as the Coleopteron shown in Fig. 67, various Lepidoptera, etc. The elongation of the maxilla may be accomplished through the lengthening of the galea, or of the stipes, or of both galea and stipes.

Figure 65 shows the condition typical of the Siphonaptera (fleas) in general, and since all of the parts are preserved in a fairly typical condition, I fail to see how there can be any uncertainty as to the interpretation of the mouthparts of the fleas. The cardo *ca* is of the endocardine type, and hence differs from the Diptera I have seen—and in fact the whole character of the maxilla of the Siphonapteron shown in Fig. 65 is more primitive than most Dipterous maxillæ (and even exhibits a marked resemblance to a Psocid's maxilla) thus indicating that the line of development of the Siphonaptera probably branched off from the ancestral Diptera while the latter had still preserved many Trichopterous and Mecopterous features. The sclerite *pf* of the flea shown in Fig. 65 probably represents the palpifer, and if this is the case, the palpifer is larger and better demarked than in any Diptera, Trichoptera, or Mecoptera I have seen. The lacinia is atrophied (as in Diptera and most Trichoptera) while the galea *ga* is suggestive of that of certain Diptera and Trichoptera. It is rather surprising that the maxillæ of most fleas are not more elongate, since most of the blood-sucking insects allied to the Siphonaptera have long slender maxillæ.

In the Trichoptera, lengthening of the maxilla may be accomplished by the lengthening of the cardo *ca* as in Fig. 62, or more rarely, by the lengthening of the galea *ga* as in Fig. 63, and the latter insect exhibits a tendency toward the lengthening of the galea which takes place to such a remarkable degree in the Lepidoptera. The Trichoptera are usually ectocardine (Figs. 62 and 64, *ca*) as is the case with most Diptera, and Hymenoptera, and in this respect the Trichoptera differ from their near relatives the Lepidoptera, which are mostly endocardine. The cardo *ca* of the Trichopteron shown in Fig. 63 (drawn from specimens given me by Mr. Banks and Dr. Betten) however, is not turned markedly inward or outward, although it might be considered endocardine, if the structure bearing the label *ca* in Fig. 63 is really the cardo. The galea *ga* of the Trichopteron shown in Fig. 62 is suggestive of the Dipterous type; while that of the Trichopteron shown in Fig. 64 is faintly suggestive of certain Hymenoptera. The maxillæ of the Trichoptera which I have studied are not as similar to the maxillæ of the Mecoptera as one might expect, and they are disappointingly unlike the maxillæ of most Neuroptera. They do resemble the maxillæ of the Diptera (with the Siphonaptera) and Hymenoptera, however, and are suggestive of the Lepidoptera in many features. The evidence of the maxillæ of the Trichoptera would therefore indicate rather close affinities with the Lepidoptera, and would point to a common ancestry with the Hymenoptera, Diptera and Siphonaptera, which may be interpreted as meaning that the Trichoptera arose from the Neuroptera-like forbears from which the Hymenoptera were derived, and their line of descent branched off with that of the Mecoptera; while the Diptera, with their derivatives the Siphonaptera, were descended from ancestors which also arose at this point.

The maxilla of a Lepidopteron such as that shown in Fig. 77 is much more primitive than any Trichopteron I have seen, and this indicates that the Lepidoptera may have arisen from ancestors more primitive than either Trichoptera or Mecoptera; and their forbears may have been more like those of the Neuroptera—although the maxilla of the Mecopteron shown in Fig. 53 is almost as primitive as that of the Lepidopteron shown in Fig. 77. The division of the cardo *ca* into basicardo *bc* and disticardo *dc* in the Lepidopteron shown in Fig. 77

denotes a persistence of a primitive Orthopteroid feature which, however, also occurs in the Neuroptera (Figs. 50 and 51) as well, and is retained even in the more highly specialized Neuroptera. The division of the galea *ga* into a basigalea *bg* and a distigalea *dg* is another primitive survival in the insect shown in Fig. 77—and a similar division is also retained in the Neuroptera (Fig. 50) as well. The huge development of the maxillary palpus *mp* in Fig. 77 is a feature which also occurs in the primitive Hymenopteron *Xyela* (not shown in Fig. 58) as well as *Philopotamus* among the Trichoptera, and is a point of similarity between these three groups, although its significance is not very important from the standpoint of phylogeny.

In the Lepidopteron shown in Fig. 78, the maxillary palpus *mp* has grown shorter as the galea *ga* grows longer, and finally in such Lepidoptera as the one shown in Fig. 79, in which the galea *ga* is hugely developed, the maxillary palpus is reduced to the small vestige bearing the label *mp*. In connection with the discussion of the maxillary palpus of the Lepidopteron shown in Fig. 78 (drawn from specimens given me by Dr. Busck), I would call attention to the outgrowth *ppr* of the basal segment of the maxillary palpus, which is unlike anything I have seen in any other insect, although it is a little suggestive of the structure labeled *ga* in Fig. 4, which I have interpreted as the galea in Fig. 4,—but this structure is not on the same side of the sclerite at the base of the maxillary palpi as the structure labeled *ppr* in Fig. 78. The palpiprocess *ppr* of the yucca moth shown in Fig. 78 occurs only in the female of this moth and it is indeed astonishing that no other insect should exhibit structures approaching it. Although the use of the organ in question for holding the pollen mass when the female moth pollenizes the yucca flower may account for its persistence and further development when once developed (since the moth has become absolutely dependent upon the yucca plant for its racial existence) we would expect some indications of the formation of a similar structure (though not so well developed) in allied insects, and when the related species have been studied with this in view, we shall doubtless be able to account for the origin of this peculiar structure which is the most remarkable that I have encountered in any insectan maxilla.[1]

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[1] Dr. Adam Boving tells me that certain Dascillid beetle larvæ have a structure comparable to this in their maxillæ.

The moth shown in Fig. 78 shows a slight indication of the formation of the paralora *pl* which is well developed in Fig. 79, and may possibly be a structure peculiar to the Lepidoptera, since I have not found it developed in exactly this fashion in the other orders examined. It appears to be developed in connection with the reduction of the labium, and very probably occurs in other insectan orders in which the labium is reduced. The folding of the galea *ga* of the insect shown in Fig. 79, may bear some relation to the peculiar folding of the galea of the Hymenoptera; but I have not yet had the opportunity of investigating this interesting subject further, although I am hoping to do so in the near future.

The maxilla of the aberrant Strepsipteran type shown in Fig. 61 (drawn from a specimen given me by Dr. Brues) is suggestive of the maxillæ of certain Trichoptera, in which the reduced maxillary palpi are about all that is left of the maxillæ. It is quite possible that certain Coleoptera will also exhibit the same phenomenon of the reduction of the maxilla to a palpus borne at the end of a ridge extending across the under side of the head in the region where the atrophied labium was formerly borne; but I have not been able to find such a Coleopteron, and the maxilla of the Strepsiptera would appear to be more like that of certain Trichoptera than any other insects, although I am inclined to regard the Strepsiptera as highly aberrant forms arising from the ancestral Coleoptera near the point of origin of the ancestors of the Hymenoptera and Trichoptera. The Strepsiptera exhibit certain features in common with the Coleoptera, Hymenoptera and Trichoptera, and the above-mentioned origin for the group is the one which best accords with the facts, although I have provisionally placed the Strepsiptera next to the Coleoptera (the usual grouping of these insects). In so placing the Strepsiptera, however, I would not minimize their annectant character between the Coleoptera on the one side, and the Hymenoptera and Trichoptera on the other.

The interrelationships of the orders of living insects indicated by the comparative morphology of various structures such as the wing-veins, mouthparts, terminal abdominal structures, etc., are briefly set forth in the following groupings, in which a few fossil forms are included because of their phylogenetic importance.

CLASS INSECTA.

- Subclass I. Apterygota.
  - Division A. Proturadelphia.
    - Superorder 1. Panprotura.
      - Orders: Protura, Collembola, etc.
  - Division B. Thysanuradelphia.
    - Superorder 1. Panthysanura.
      - Orders: Lepismatoida, Machiloida, etc. The Campodeioida (including the Japygids) may be included here or may be placed in a separate superorder.
- Subclass II. Pterygota.
  - Division A. Archipteradelphia.
    - Superorder 1. Panpalæodictyoptera.
      - Orders: Palæodictyoptera and a number of fossil forms.
    - Superorder 2. Panarchiptera.
      - Orders: Protephemeroida, Ephemeroida (Archiptera), Odonata, etc.
  - Division B. Orthopteradelphia.
    - Superorder 1. Panisoptera.
      - Orders: Protoblattoida, Blattoida, Mantoida (possibly a part of the Blattid order), Isoptera, etc.
    - Superorder 2. Panorthoptera.
      - Orders: Protorthoptera, Orthoptera (s. str.), Phasmoida, Dermaptera, etc. The preceding superorder might be included in this superorder also.
    - Superorder 3. Panplecoptera.
      - Orders: Plecoptera, Embiidina, etc.
  - Division C. Neuropteradelphia.
    - Superorder 1. Panhemiptera.
      - Orders: Psocoida, Hemiptera (including Homoptera), Thysanoptera, Anoplura, Mallophaga, etc.
    - Superorder 2. Panneuroptera.
      - Orders: Neuroptera, Hymenoptera, Coleoptera, etc. The Strepsiptera may also be included here.
    - Superorder 3. Panmecoptera.
      - Orders: Mecoptera, Diptera, Siphonaptera, Trichoptera, Lepidoptera, etc. This superorder might be included in the preceding one.

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Packard's "Textbook"; Berlese's "Gli Insetti"; an article by Crampton, 1921, Annals Ent. Soc. America, 14, p. 65; and the excellent article on the mandibulate insects by Waterhouse, 1895. The voluminous publications of Chatin are of less value. For the special groups, the following are of interest.

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ABBREVIATIONS.

a, laciniadentes, or apical tooth-like processes.
b, midappendix, or modified lacinula.
bc, basicardo, or basal sclerite of cardo.
be, endite of second segment of crustacean appendage.
bg, basigalea, or basal segment of galea.
bl, basilacinia, or basal sclerite of lacinia.
bm, basimaxilla, or basal plate of maxilla.
bp, basipodite, or second segment of crustacean appendage.
bs, basistipes, or basal sclerite of stipes.
ca, cardo.
cc, cardocondyle.
cm, cardomargin.
cp, coxopodite, or first segment of crustacean appendage.
cpr, cardoprocess.
crp, carpopodite, or fifth segment of crustacean limb.
ct, cardotendons.
dc, disticardo, or distal sclerite of cardo.
dg, distigalea, or distal segment of galea.
dig, digitus.
dl, distilacinia, or distal sclerite ("head") of lacinia.
dp, dactylopodite, or seventh segment of crustacean limb.
ds, dististipes, or distal sclerite of stipes.
en, endopodite, or palpus.
eng, endogalea, or inner lobe of galea.
eus, eustipes.
exg, exogalea, or outer lobe of galea.
f, "fulturæ."
ga, galea.

hp, hypopharynx.
ie, endite of fourth segment of crustacean appendage.
il, interlora, or bar connecting maxilla with hypopharynx.
ip, ischiopodite or third segment of crustacean limb.
la, lacinia.
le, lacinulæ (modified spines or setæ).
lf, laciniafer, or lacinia-bearing sclerite.
li, labium.
md, mandible.
me, meropodite, or fourth segment of crustacean limb.
mm, micromere, or small palpal segment.
mp, maxillary palpus (endopodite).
ms, mediostipes, or median area of stipes.
mx, maxilla.
pas, parastipes.
pf, palpifer.
pl, paralora.
pp, propodite, or sixth segment of crustacean limb.
ppr, palpiprocess, or process of basal segment of palpus.
so, sense organ on third segment of maxillary palpus.
st, stipes.

EXPLANATION OF PLATES XII–XVII.

All figures are of the insect's right maxilla drawn from the posterior (ventral) surface. The following figures were redrawn from others: Figs. 6, 8, 11, 12, 14, 15, 20, 21, 24, and 25 from Boerner; 7 and 9 from Escherich; 13 from Stummer-Traunfels; 17 from Racovitza; 19 from Imms; 22 from Prell; 29 from Desneux; 66 from Tetley; 76 from Enderlein; 72 from Peterson, and 74 from Snodgrass.

FIG. 1. Lines of descent of insects and their arthropodan relatives.

FIG. 2. Maxilla of amphipod crustacean *Gammarus ornatus*.

FIG. 3. Maxilliped of *Gammarus* sp.

FIG. 4. Maxilla of larval Neuropteron *Sialis* sp.

FIG. 5. Maxilla of larval Coleopteron *Passalus* sp.

FIG. 6. Distilacinia of Sminthurid Collembolan *Sminthurides serroseta*.

FIG. 7. Lacinia of Lepismatid Apterygotan *Nicoletia neotropicalis*.

FIG. 8. Distilacinia of Sminthurid Collembolan *Allacma fusca*.

FIG. 9. Lacinia of Lepismatid Apterygotan *Assmuthia spinossisima*.

FIG. 10. Maxilla of *Lepisma* sp.

FIG. 11. Distilacinia of the Podurid Collembolan *Anurida maritima*.

FIG. 12. Same from another view.

FIG. 13. Maxilla of Apterygotan *Campodea staphylinus*.

FIG. 14. Distilacinia of Entomobryid Collembolan *Pogognathus plumbeus*.

FIG. 15. Distilacinia of Apterygotan *Machilis* sp.

FIG. 16. Maxilla of Chilopod *Scolopendra* sp.

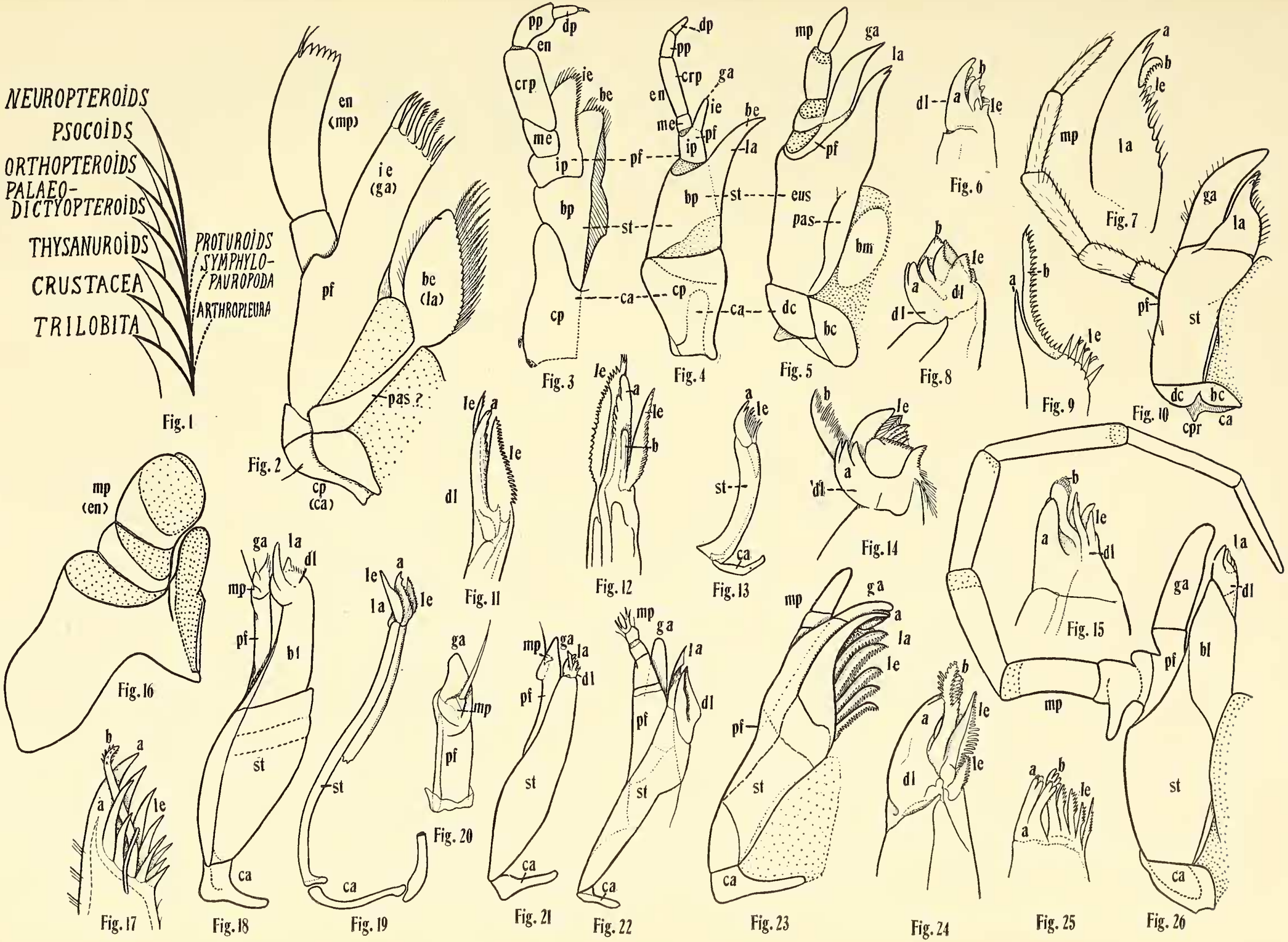
FIG. 17. Endite of maxilla of Crustacean *Trichoniscus corsicus*.

FIG. 18. Maxilla of *Tomocerus flavesceus* (Entomobryid Collembolan).

FIG. 19. Maxilla of Podurid Collembolan *Anurida maritima*.

FIG. 20. Palpifer, galea, and palpus of maxilla of Podurid Collembolan *Tetrodontophora bielanensis*.

Fig. 21. Maxilla of same.
Fig. 22. Maxilla of Proturan *Eosentomon* sp.
Fig. 23. Maxilla of Apterygotan *Japyx* sp.
Fig. 24. Distilacinia of Podurid Collembolan *Tetrodontophora bielanensis.*
Fig. 25. Second endite of maxilla of Crustacean *Gammarus* sp.
Fig. 26. Maxilla of Apterygotan *Machilis* sp.
Fig. 27. Leptinid Coleopteron *Leptinus testaceus.*
Fig. 28. Hemimerid Dermapteron *Hemimerus talpoides.*
Fig. 29. Leptinid Coleopteron *Platypsyllus castoris.*
Fig. 30. Immature Odonatan *Æschna umbrosa.*
Fig. 31. Immature Ephemerid *Oniscigaster* sp.
Fig. 32. Tettigoniid Orthopteron *Peranabras scabricollis.*
Fig. 33. Grylloid Orthopteron *Gryllus* sp.
Fig. 34. Grylloid Orthopteron *Gryllotalpa* sp.
Fig. 35. Dermapteron *Anisolabis maritima.*
Fig. 36. Staphylinid Coleopteron.
Fig. 37. Cicindelid Coleopteron *Cicindela* sp.
Fig. 38. Zorotypoid Psocid *Zorotypus snyderi.*
Fig. 39. Phasmid Orthopteroid *Timema* sp.
Fig. 40. Embiid *Oligotoma* sp.
Fig. 41. Grylloblattid Orthopteron *Grylloblatta campodeiformis.*
Fig. 42. Tridactyloid Orthopteron *Rhipipteryx atra.*
Fig. 43. *Tettix* sp.
Fig. 44. Plecopteron *Eusthenia* sp.
Fig. 45. Isopteron *Termes* sp. from Belgian Congo.
Fig. 46. Immature Plecopteron *Perla* sp.
Fig. 47. Blattid *Periplaneta americana.*
Fig. 48. Mantid *Stagmomantis carolina.*
Fig. 49. Neuropteron *Corydalis cornutus.*
Fig. 50. Neuropteron *Ululodes* sp.
Fig. 51. Neuropteron *Nemoptera* sp.
Fig. 52. Mecopteron *Bittacus* sp.
Fig. 53. Mecopteron *Panorpodes* sp.
Fig. 54. Hymenopteron *Lyda hypotrophica.*
Fig. 55. Hymenopteron *Chlorion ichneumonium.*
Fig. 56. Hymenopteron *Pelecinus* sp.
Fig. 57. Phasmid *Anisomorpha* sp.
Fig. 58. Hymenopteron *Xyela* sp.
Fig. 59. Hymenopteron *Macroxyela* sp.
Fig. 60. Mecopteron *Panorpa* sp.
Fig. 61. Strepsipteron *Xenos* sp.
Fig. 62. Trichopteron *Plectrotarsus gravenhorsti.*
Fig. 63. Trichopteron *Dipseudopsis* (from the Himalayas).
Fig. 64. Trichopteron, *Neuronia semifasciata.*
Fig. 65. Siphonapteron *Pulex* sp.



MAXILLAE OF INSECTS.